SYNOPSIS OF A REVIEW OF THE GENERA OF RECENT AND TERTIARY MACTRIDÆ AND MESODESMATIDÆ.

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In the course of some palæontological work upon which I have been engaged during the past year, it became necessary to review the Mactracea, which were found to be in a good deal of confusion, both as regards systematic relations and nomenclature. As a result I have been obliged to examine all the accessible material, conchological and anatomical, and contemplated offering to the Society a synopsis of my conclusions.

I soon found that, if I attempted to include diagnostic characters, this synopsis would reach inconvenient bulk for the Society's Proceedings, besides requiring an excessive amount of explanation. The hinge of *Mactra* has been so superficially studied, for the most part, that in order to avoid tedious periphrasis it became necessary to classify and name its several parts and investigate their dynamic relations. The Pelecypod hinge is an organic machine for the attainment of certain physical results, and the course of its development and modification is very closely connected with the stresses and strains to which it, considered as a piece of mechanism, is subjected. The questions involved are still further complicated in this group by the descent of a portion of the primitive ligament through the hinge margin, and its modification to form an internal "cartilage."[1] Every stage of the process is beautifully illustrated in one or another genus of the Mactracea, from that in which the resilium is barely detached from its parent ligament (as in *Spisula*); or has developed a shelly barrier between the two (*Mactra* s.s.); or exemplifies the descent of the ligament after the resilium, though not in the same cavity (*Cyclomactra*); or, finally, the total immersion of both parts and their enclosure in a common receptacle (*Mulinia* and *Rangia*). The process is not only illustrated in its various stages by existing Mactroid animals, but the succession of the fossil forms, from the Chalk to the present day, gives us what we may permissibly recognize as a serial succession of changes along a common line of descent, in

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[1] Since this substance is totally different from cartilage, properly so-called, and the ligament is sometimes also internal, it seems desirable to substitute a new name for the part in question. Its function being invariably that of separating the valves by its expansional elasticity, I have decided to adopt for it the name *resilium*, while, for the pit in which it is frequently seated, we may retain the term *chondrophore* already widely used.

which several of the more distinct types of the present fauna may be traced to their inception.

These facts I hope to fully exemplify in the final part of my "Tertiary Mollusks of Florida," which will probably be ready for publication in the course of the next year.

I have therefore decided to offer to the Society a table of the resulting classification, giving the families, sub-families, and genera of the Mactracea, together with the types upon which the subdivisions are founded; accompanied by a statement of the characters of the families and sub-families, and of the nomenclature I have adopted for the different parts of the hinge. This will enable me to receive the criticisms of members and others interested, and thus perfect my final arrangement, which will be adequately illustrated.

To those whose knowledge of the group is chiefly gained from existing text-books I fear the first impression will be that an undue multiplication of subdivisions has been proposed. As a matter of fact, I have suppressed about as many subdivisions as I have adopted, and, if anyone will attempt to state in tabular form the characteristics of a full series of species, it will be found, I believe, that the subdivisions here adopted are an aid to clear comprehension of the various modifications, and enable relationships of form and geographical distribution to be comprehended in a manner impossible under the old classification.

The hinge of the group, which I have called Teleodesmacea, including the majority of recent Pelecypods, is characterized by an alternation of the teeth of the two valves, so that, when the valves are open, the series in each is composed of teeth separated by spaces, into which those of the other valve fit when closed. Shells with this arrangement have been named Heterodonta by Neumayr. He referred the typical Mactracea to another group which he characterized as having vacant spaces in one valve which no tooth exists in the other valve to fill, and which group he named Desmodonta. Thus, if the inferior Λ-shaped tooth of *Mactra* be regarded as a coalescence at the top of two originally separate teeth, the space between the arms receiving no tooth from the opposite valve would conform to the Desmodont definition. But, as I have shown in my recent "Monograph of the genus *Gnathodon*" [=*Rangia*],[1] and more fully in my forthcoming Florida report, this tooth is really a single tooth, dynamically modified to fit the superior Λ-shaped cardinal, and the latter is really composed of two primitive (and still not always coalescent) teeth, and therefore the hinge is of the Heterodont, and not of the Desmodont, type.[2]

To fully understand the mechanism and development of the Mactroid hinge one must give a careful study to its minute details. It is only when one finds characters, which would seem at first sight very

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[1] Proc. U.S. Nat Mus. xvii. (1894) pp. 89–106.

[2] Bittner has recently worked out the same conclusion in a critique on some of Neumayr's views: Ueber die syst. Stellung von *Mactra*, Verh. k.k. geol. Reichsanstalt, 1892, pp. 232–240.

trifling, rigidly preserved through long ages of geological time, and their modification accomplished only when the whole organism has submitted to important changes, that one begins to realize that the prominence of a feature is not always the best index to its systematic value, and that there is literally no possibility of knowing any organism too thoroughly.

In a typical *Mactra*, well developed and unbroken, the hinge presents the following characteristic armature:[1] a cartilage pit or chondrophore; a group of teeth usually called cardinals, comprising true teeth, and often accessory lamellæ formed in sinuses of the mantle-edge, but not necessarily belonging to the normal type of dentition; and the so-called lateral teeth, with laminæ in the opposite valve between which the lateral is received. Taken by valves: *In the right valve.*—An anterior and a posterior pair of lateral laminæ; a more or less coalescent pair of cardinal teeth, adjacent above and distant below, forming a ∧, each arm of which may, or may not, be attended by a delicate accessory lamella parallel to the arm. *In the left valve.*—An anterior and posterior lateral; a single ∧-shaped cardinal, with or without an accessory lamella on each side of it.

When a series of species is compared, it will be seen that the ∧ rotates, so to speak, on its apex, while preserving its apical angle tolerably uniform, in each of the different species. In one the anterior arm may be appressed against the dorsal shell-margin, while the posterior arm is separated from the verge of the chondrophore by a considerable space; in another the posterior arm may project over the cavity of the pit, and a wide sinus appear between the anterior arm and the dorsal margin; or, again (as in *Mactrotoma*), the arm of the cardinal, the accessory lamella, and one of the lateral laminæ may be compressed into one radial line, so as to present the appearance of a single tooth with three serrations. In typical Mactroids, above the apex of the chondrophore, the anterior end of the ligament recedes laterally to the point of the umbo. The space between this apex of the ligament and the middle line between the valves is occupied in each valve by a small shelly point, which I call the *spur*: this is greatly exaggerated in the African *Schizodesma*, and in more normal forms is frequently associated with a flat plate which roofs over the apex of the chondrophore. According to the development of the spur and the distance between the beaks of the valves, the diverging anterior ends of the ligament may be far apart, near, or not perceptibly divided. When well marked, the ligament from above has the appearance of a barbed arrow-head, or, as I have named it, is sagittate. Behind and above the cartilage-pit is the scar of attachment of the ligament, walled off in typical Mactroids from the pit by a shelly barrier, which is absent in the Spisuloid forms. I term the pair of projections in the

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[1] I prefer to use plain English terms with a special signification, rather than propose new names of classical derivation, because it is easier for the mind to appreciate new things when it is not simultaneously burdened by having to remember a new vocabulary.

right valve which receive the lateral teeth of the left valve between them "laminæ," and only the laterals of the left valve "laterals"; by keeping to which plan a good deal of verbiage is avoided, and the meaning is made clearer. The angular space between the anterior arm of the cardinal tooth and the dorsal margin of the valve I call the "anterior sinus" of the hinge, and the other, behind the chondrophore, the "posterior sinus." The space between the arms of the cardinal tooth is the "ventral sinus."

When shell-matter is being secreted from the pallial surface for the growth of the hinge, there are some unoccupied crevices to which it may penetrate by capillary action. One such is between the side of the cardinal tooth and the surface of the resilium in the left valve; others are parallel to the arms of the cardinal tooth in the right valve. In these places thin sheets of shelly matter may be deposited which I call "accessory lamellæ," which are often confounded in descriptions with true teeth. They are, as might be expected, excessively fragile and very inconstant; sometimes they exist unattached, like a species of pearl. To the presence of these lamellæ is due the ascription, in old works, of three cardinal teeth to the valve in *Mactra*. Really there is one true cardinal in the left and two in the right valve, normally, in this group; to which may be added an anterior and posterior accessory lamella in the left, and an anterior accessory lamella in the right valve; all of which lamellæ may be present, and any one of which may be absent in any species, or in some individuals of any species; though the anterior lamellæ are tolerably constant. These lamellæ may be attached to the hinge-plate by a slender peduncle, may be solidly rooted like a true tooth, or may be mounted upon the edge or side of a lateral tooth and coalescent with it. In the latter case a close and intelligent inspection will almost always result in the detection of the elements belonging to the tooth and to the lamella respectively. In *Mactrotoma* we have the most marked instance of this, since in the right valve the anterior lamella is mounted on the back of the ventral lamina, and the anterior arm of the cardinal is (in its turn) mounted on the back of the accessory lamella. A profile view shows the upturned point of each still remaining separate; while a vertical view reveals the sutures at which the separate masses coalesced. In the left valve only the lamella and the anterior lateral are coalescent.

When the hinge-plate is very obliquely set on to the shell, as in *Mactra alata*, Spengler, the thin and slender cardinal teeth are sometimes reinforced by horizontal or vertical "buttresses," which extend from the teeth to the hinge-margin. In using adjectives denoting the direction of plane surfaces in description, I conceive of the shell as suspended by the beaks of the valves, with its longer antero-posterior line in a horizontal plane. When, therefore, the buttress extends in a plane substantially parallel with the plane which includes the margin of the valves it may cover part of the sinus, so that the portion covered is either wholly filled with shelly matter, or is merely "roofed over" with a shelly plate. The former condition is more common. In other cases the buttresses may extend in a plane at right angles to

the plane of the valves, and inclined at any angle to the plane of their transverse diameter which will give the greatest strength with the least expenditure of material. Such buttresses cut the sinus into two or more cavities, those nearest the beak being cellular. This variety of buttress I call a "septum." It occurs in *Mactrella*, but is somewhat rare, and, when present, curiously complicates the hinge.

The initiation of hinge-teeth is illustrated in a curious way in *Schizodesma Spengleri*, where the ridge supporting the ligament is produced at the margin of the valve into an obscure prominence which is partly received by a slight depression in the opposite valve. This requires only a little encouragement to develop into an entirely new type of tooth, at least compared with the normally present teeth of the hinge of *Mactra*.

With the separation of the primitive ligament into ligament and resilium, a more or less marked space often intervened between their adjacent sides. In the typical Mactras, this space has become more or less occupied by a shelly ridge, which, when the valves are closed, partially cuts off the ligament from the resilium. This ridge, or shelly wall, naturally belongs to the posterior slope of the shell, and may become coalescent, over the chondrophore, with the spur. In a small antipodean group of species the partition is accomplished in another way. The spur projects, and is continued as a more or less irregular shelly rod, which is laid close to the ventral border of the ligament, and is attached to the shell, though not thoroughly coalescent. *Mactra ovata*, Gray, offers a good example of this formation. In a single species (which appears to be *M. tristis*, Gray, of Reeve's Conch. Iconica) the ligament, while quite separate from the chondrophore, has itself sunk below the dorsal shell-margin, only its most anterior point remaining at the surface.

The shelly portions of the hinge arise from a shelly basis stretched antero-posteriorly between the limbs of the arch forming the cardinal margin. This basis is called the *hinge-plate*, and it may have its surface "flat," *i.e.* nearly parallel to a vertical plane between the valve margins, or "oblique," that is inclined at an angle, so that its dorsal edge starts from the valve some distance from the dorsal margin of the latter. When the hinge-plate forms a marked angle with the valve, the space between the ventral edge of the plate and the dorsal margin of the valve is said to be "excavated," forming a Λ-shaped valley on each side of the chondrophore; a state of things some of the older writers have tried to indicate by the objectionable expression that the hinge is "double-edged." In *Mactra* the hinge-plate is never perfectly flat (as we find it, for instance, in *Astarte*); and in some of the thin-shelled forms, like *Pteropsis* or *Labiosa*, the excavation is deep and sharp, and is indicated on internal casts of the fossils by two areas set off from the general mass by deeply incised lines. A hinge-plate is always present, however, and we never find a Mactroid hinge set directly on the margin of the valve as in *Arca*. In some very thin and small forms the edge of the hinge-plate itself is turned up, and becomes patulous to form the laterals (*Raetella*).

The diverging, more or less coalescent, primitive teeth which form

the superior cardinal (always in the right valve, normally) I call the "arms" of the cardinal tooth. The single tooth of the left valve has sometimes developed corresponding arms, but otherwise may be thick, triangular, grooved below in the middle, and turned up like the petal of a lily. This latter condition I call "petaloid." It is conspicuous in some forms of *Spisula*. In some Mactroids with deeply excavated hinge-plate the sinus is roofed over, and a bristle may be inserted into a deep cavity nearly to the beaks. While the dorsal lamina is set on the valve, the ventral lamina arises from the plate; both are elegantly arched and somewhat twisted. This may be well observed in *Cœlomactra violacea*.

Having endeavoured to give some idea of the diversity of character to be found in the hinge-apparatus of *Mactra*, which can only be adequately studied specimens in hand, it remains to observe that in a very complete series of fossil forms, taken with the recent ones, it will be found that the various types closely approach one another by the agency of border species. This is what we find in all groups of animals when sufficiently full series are studied, and what, by the theory of evolution, we ought to expect. In all large groups it becomes necessary to name what may be called, with reference to the group, the successive stages, in order that they may be adequately recognized, and this is what, in the accompanying schedule, I have attempted. It is only just to acknowledge that a long step was taken in this direction so far back as 1853, by Dr. J. E. Gray, and, save for some errors of identification, the system of to-day was quite fully indicated in its principal features in his classification.

The following characters are those which I find in the different larger groups under consideration; though, of course, there are numerous cases where it has been impracticable for me to obtain the soft parts of species, which I have consequently been obliged to classify by the shell.

Family MACTRIDÆ.[1]

Siphons united to their tips.

Subfamily MACTRINÆ.

Shell subequilateral, nearly closed; hinge normal (as above described), fully developed; siphons partially or wholly naked, and wholly retractile within the shell; mantle lobes separated ventrally between the siphons and the anterior adductor.

Subfamily PTEROPSIDINÆ.

Shell subequilateral, nearly closed; hinge feeble, concentrated; the laterals much reduced or partly obsolete; siphons wholly retractile, naked; mantle partially closed ventrally.

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[1] Only differential characters are mentioned under the family names.

Subfamily LUTRARIINÆ.

Shell inequilateral, widely gaping; hinge tending to be irregular, concentrated; the laterals partly reduced, or obsolete; the cartilage-pit free, in the plane of the hinge-plate. Siphons contractile, not retractile within the shell, clothed with a horny epidermis to their tips; ventral opening of the mantle short, and the foot correspondingly reduced in size.

Subfamily ZENATIINÆ.

Shell inequilateral, compressed; hinge concentrated, irregular, the laterals tending to become obsolete, or absent; chondrophore bent out of the plane of the hinge-plate, and more or less adherent to the valve; siphons retractile? Ventral opening of the mantle and foot much reduced.

? Subfamily ANATINELLINÆ.[1]

Shell inflated, gaping, radiately sculptured; hinge with a prominent narrow chondrophore, a short external ligament, a narrow cardinal and an accessory lamella in each valve, without laterals; pallial line without a sinus; soft parts unknown; siphons probably short.

Family MESODESMATIDÆ.

Retractile, naked, siphons more or less completely separated; shells cuneiform, more or less compressed, and disproportionately heavy.

Subfamily MESODESMATINÆ.

Shells with a pallial sinus, porcellanous texture, with a conspicuous periostracum; ligament inconspicuous, and, if wholly external, more or less degenerate, otherwise as in *Spisula*; resilium narrow, oblique; recent species with a single, narrow, long, left cardinal tooth, with a short posterior arm extended across the apex of the cartilage-pit; right cardinal lamella feeble, nearly obsolete in the recent species, but normal in the Eocene forms.

Subfamily DAVILINÆ.

Pallial line simple; shells more rounded than in the preceding subfamily, but the other characters similar; siphons probably short.

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[1] I have not been able to examine the genus *Cardilia*.

Subfamily ERVILIINÆ.

Shells small, thin, equilateral; ligament marginal, obsolete or absent; resilium small; hinge much concentrated; the lateral teeth small; the dorsal anterior lamina absent, the ventral more or less coalescent with the anterior arm of the right cardinal; left cardinal large, bifid; pallial sinus well marked.

There is some doubt as to the characters of the soft parts of *Cæcella*, but so far as the shell goes it is simply a large brackish-water *Ervilia*, and if the latter belongs to the Mesodesmatidæ so does the former.

There are some curious parallelisms in the characters of the different groups above mentioned. They cannot all be tabulated in one scheme, but offer some points worthy of investigation.

Theoretically, after the division of the primitive ligament into ligament and resilium, the order of modification should have followed two lines—one in which the parts, though separated, are not walled apart by a shelly septum, and hence the possibilities of modification are still left unlimited, and the other, where the separation has been made final by the development of a shelly partition. In accordance with this hypothesis we find the oldest fossil Mactridæ Spisuloid and even without a solid base of attachment for the ligament proper; later this base is supplied, and certain forms assume the Mactroid type. *Pteropsis* is the earliest known genus of its subfamily, and is Spisuloid, while the recent *Raëta* is Mactroid. The older *Lutraria*, and the newer *Tresus*, the ancient *Standella*, and the modern *Heterocardia*, offer parallel cases. The Zenatiinæ appear to be a relatively modern type, and are all Spisuloid; as is *Anatinella*. In each case the Mactroid features belong to the later stage of each group, when they are present at all, some groups not having yet acquired the requisite equilibrium. The Mesozoic forms, so far as known, have the *Cymbophora* hinge; the Eocene ones, in America, are Spisuloid. Later, in the Miocene, comes total submergence in *Mulinia* and *Rangia*, while none of the aberrant later developments have reached the Mactroid stage. These features may be tabulated as follows, for the Mactridæ:—

Ligament:	Spisuloid.	Submerged.	Mactroid.
Mactrinæ	*Spisula.*	*Mulinia.*	*Mactra.*
	Spisula.	*Rangia.*	*Mactra.*
	Hemimactra.	*Rangianella.*	*Mactrotoma.*
	Cymbophora.	*Miorangia.*	*Mactroderma.*
	Schizodesma.	—	*Cœtomactra.*
	Leptospisula.	—	*Mactrella.*
Pteropsidinæ	*Pteropsis.*	—	*Labiosa.*
	—	—	*Raëta.*
	—	—	*Raëtella.*
Lutrariinæ	*Lutraria.*	—	*Tresus.*
	Standella.	—	*Heterocardia.*
	Eastonia.	—	—
Zenatiinæ	*Zenatia.*	—	—
	Resania.	—	—
	Darina.	—	—
Anatinellinæ	*Anatinella.*	—	—

SYSTEMATIC TABLE OF THE GROUPS.

Family MACTRIDÆ.

Subfamily MACTRINÆ.

Genus MACTRA (Linné), Lam., 1799.
Type.—M. stultorum, L.

Subgenus *Cœlomactra*, Dall. *Type.—M. violacea* (Ch.), Gmelin.
Subgenus *Mactroderma*, Dall, 1894. *Type.—M. velata*, Phil.

Section *Mactroderma*, s.s. *M. velata*, Phil.
Section *Cyclomactra*, Dall. *M. tristis*, Gray.

Subgenus *Mactrotoma*, Dall, 1894. *Type.—M. fragilis*, Gmel.

Section *Simomactra*, Dall. *M. dolabriformis*, Conr.
Section *Micromactra*, Dall. *M. californica*, Conr.

Subgenus *Mactrella* (Gray), Dall, 1894. *Type.—M. alata*, Spengler.

Section *Mactrella*, s.s. *M. alata*, Spengler.
Section *Harvella*, Gray, 1853. *M. elegans*, Sby.
Section *Mactrinula*, Gray, 1853. *M. plicataria*, Lam.

Genus SPISULA, Gray, 1838.
Type.—Mactra solida (L.), Gray, 1847.

Subgenus *Hemimactra*, Swn., 1840. *Type.—M. solidissima*, Dillwyn.

Section *Mactromeris*, Conr., 1868. *M. polynyma*, Stm.
Section *Pseudocardium*, Gabb, 1869. Miocene: *Cardium Gabbi*, Rem.
Section *Oxyperas*, Mörch, 1853. *M. triangularis*, Lam.

Subgenus *Leptospisula*, Dall, 1894. *Type.—M. striatella*, Lam.
Subgenus *Cymbophora*, Gabb, 1869. Cretaceous. *Type.—Mactra Ashburneri*, Gabb, Cala.
Subgenus *Schizodesma*, Gray, 1837. *Type.—M. Spengleri*, Linné.

Genus MULINIA, Gray, 1831.
Type.—M. typica, Gray (=*edulis*, King).

Genus RANGIA, C. Des Moulins, 1832.
[*Gnathodon*, Gray, 1831, *non* Goldfuss, 1820 (Pisces).]
Type.—R. cyrenoides, Desm.

Subgenus *Rangianella*, Conrad, 1868. *Type.—Mactra mendica*, Gould.

Section *Miorangia*, Dall. *M. Johnsoni*, Dall.

Subfamily PTEROPSIDINÆ.

Genus Pteropsis, Conrad, 1860. Eocene.
Type.—Lutraria papyria, Conr.

Genus Labiosa (Schmidt), Möller, 1832.
Type.—Mactra anatina, Spengler.

Subgenus *Raëta*, Gray, 1853. *Type.—Lutraria canaliculata*, Say.

Section *Raëtina*, Dall. *R. indica*, Dall, n.s.

Subgenus *Raëtella*, Dall. *Type.—R. tenuis* (Hinds MS.), Dall.

Subfamily LUTRARIINÆ.

Genus Lutraria, Lam., 1799.
Type.—L. oblonga, Gmel., sp.

Section *Lutraria*, s.s. *L. oblonga*, Gmelin.
Section *Goniomactra*, C. Mayer. *L. impar*, Desh.
Section *Lutrophora*, Dall. *L. complanata*, Gmel.

Genus Tresus, Gray, 1853.
Type.—T. Nuttallii, Conr. (*Schizothærus*).

Genus Standella, Gray, 1853.
Type.—Mactra fragilis, Gray, *non* Chemnitz = *M. pellucida* (Ch.), Gmelin (*non Standella*, H. & A. Ads.).

Subgenus *Eastonia*, Gray, 1853. *Type.—Mactra rugosa*, Gmelin.

Genus Heterocardia, Deshayes, 1854.
Type.—H. gibbosula (Desh.), Adams.

Subfamily ZENATIINÆ.

Genus Zenatia, Gray, 1853.
Type.—Z. acinaces, Quoy and Gaim., sp.

Genus Resania, Gray, 1853.
Type.—R. lanceolata, Gray.

Genus Darina, Gray, 1853.
Type.—D. solenoides, King, sp., *non* Lam.

? Subfamily ANATINELLINÆ.

Genus ANATINELLA, Sowerby, 1834.

Type.—A. Sibbaldii, Sby.

Family MESODESMATIDÆ.

Subfamily MESODESMATINÆ.

Genus MACTROPSIS, Conrad, 1854. Eocene.

Type.—M. æquorea, Conrad.

Genus ATACTODEA, Dall.

[*Paphia*, Lam.; *Erycina*, Sby.; *Eryx*, Swainson, etc., preoccupied names in Zoology.]

Type.—Paphia glabrata, Lam.

Genus MESODESMA, Deshayes, 1830.

Type.—M. donacium, Lam., sp.

Subgenus *Mesodesma*, s.s. *Type.—M. donacium.*
Subgenus *Donacilla* (Lam.), Philippi, 1836. *Type.—M. corneum*, Poli, sp.
Subgenus *Taria*, Gray, 1853. *Type.—M. Stokesii*, Gray.
Subgenus *Paphies*, Lesson, 1830. *Type.—M. australis*, Gmel.

Subfamily DAVILINÆ.

Genus DAVILA, Gray, 1853.

Type.—D. polita, Gray.

Genus ANAPELLA, Dall.

[*Anapa*, Gray, 1853,[1] *non* Gray, 1847.]

Type.—Anapa triquetra, Hanley.

Subfamily ERVILIINÆ.

Genus ERVILIA, Turton, 1822.

Type.—Mya nitens, Montagu.

Genus CÆCELLA, Gray, 1853.

Type.—C. Horsfieldii, Gray.

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[1] N.B.—The original *Anapa* was founded on *Erycina petitiana*, Rec. = *Lasea rubra*.